THE AFFINITIES OF HALCYORNIS FROM THE LOWER EOCENE

By C. J. O. HARRISON & C. A. WALKER

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SYNOPSIS

Halcyornis toliapicus (Koenig) of the Lower Eocene, known from a single cranium, has been classified with the gulls (Koenig, 1825 and Lydekker, 1891) and the kingfishers (Owen, 1846). The specimen has now been fully prepared; it is redescribed here and its probable affinities re-appraised on the characters now apparent.

A comparison with Recent forms indicates a general similarity to skulls of Coraciiformes and Piciformes. A more detailed examination of a range of species representing families within those two orders indicates that the greatest similarity is to the Coraciiformes, particularly to the rollers of the Coraciidae and Leptosomatidae. The characters of the fossil specimen do not appear to indicate stronger affinities with either one of those families, however, and it is therefore proposed that *Halcyornis* should be regarded as the type- (and only known) genus of a new family within the Coraciiformes. A diagnosis is given of the Halcyornithidae.

I. HISTORICAL INTRODUCTION

In the earlier part of the 19th century the cranial portion of a small bird skull was found in the London Clay, Ypresian (Lower Eocene) of the Isle of Sheppey, Kent, England. It was figured by Koenig (1825), who noted the general resemblance of the rounded cranium with its even, tapering temporal fossae to that of some of the smaller gulls (e.g. Larus canus or L. ridibundus) and therefore reconstructed it as a small gull, calling it Larus toliapicus.

Owen examined the specimen, and noted (1846:554) the absence of the supraorbital grooves which accommodate the lacrimal glands (grooves which are normally present in, and typical of, gulls and most other sea-birds). He compared the specimen with Recent material but may have used an incomplete collection. He noted the resemblance of the temporal fossae to those of the kingfisher, *Alcedo atthis* (although in the latter the fossae extend upwards until they almost meet in the midline) and, believing that it was probably an early kingfisher, called it, 'Halcyornis toliapicus. Bird probably of the family Halcyonidae'. The kingfisher family is now known as the Alcedinidae. Lydekker (1891: 183) considered the specimen to be a gull. He rejected Owen's suggestion because the temporal fossae on the posterior part of the cranium were further apart than in the kingfisher; and also because of the narrowness of the interorbital bar formed by the frontal bones. He commented that, 'the imperfection of the fronto-parietal region renders it difficult to be sure as to the presence of superorbital grooves, but the appearance suggests their presence'. He associated with the skull the distal end of a left humerus (BMNH No. A 10) which he considered to be of larid origin. There appears to be no reason for associating the humerus with the cranium; the former has therefore been considered as a separate specimen and has not been dealt with in the present paper.

We have compared *Halcyornis* with a range of Recent bird bones in the British Museum (Natural History). The most obvious character, and the one on which earlier identifications were based, is the presence of well-defined temporal fossae which occupy about two-thirds of the total width of the cranium. They are of fairly even shape, tapering posteriorly, with a slightly concave posterior margin. The search for similar Recent species showing this type of posteriorly-rounded cranium with relatively simple temporal fossae produced a number of alternative possibilities, allowance having been made for a reasonable degree of variation. Specimens with some similarity were found in the Procellariidae (Procellariiformes), Fregatidae (Pelecaniformes), Rhinochetidae (Gruiformes), Laridae (Charadriiformes), Cuculidae (Cuculiformes), Alcedinidae, Momotidae, Meropidae, Coraciidae, Upupidae, Leptosomatidae (Coraciiformes), Galbulidae, Bucconidae, Capitonidae, and Ramphastidae (Piciformes). So many families possess this type of skull that it is obviously an unsatisfactory character from the taxonomic point of view, but nevertheless provides an initial limited list of potentially related families

II. DESCRIPTION AND STATE OF PRESERVATION

It was necessary to consider the other characters of the specimen, which was further prepared for this purpose, making some of the interorbital features more apparent.

The specimen consists of the posterior portion of a cranium, imperfect in all its aspects. The roof has been broken away to show part of the endocranial cast and the anterior region is broken off about half-way along the frontals. The interorbital bar is narrow; the orbital rim is apparently undamaged, with no evidence of any superorbital grooves. There is a fairly large, well-marked temporal fossa the margin of which arises anteriorly at the junction between the postorbital processes and the orbital rim, runs obliquely backwards towards the mid-line, and then curves round to pass outwards along the dorsal border of the occiput.

In lateral view the skull shows a cranium that is not particularly inflated or rounded, and the thick interorbital septum is perforated only by a single foramen for the optic nerve. This foramen is situated at the postero-ventral corner and is rather small. The orbital rim is raised slightly above the plane of the skull roof. The postorbital processes are broken on both sides, but would have been blade-like, with

narrow edges directed laterally. The temporal fossa forms, in this aspect, a well-marked groove between the postorbital process and the tympanic cavity.

The palatal surface is eroded and much of the detail on the basiparasphenoid region has been lost. The rostroparasphenoid is thick and the alaparasphenoids swing out to form a wide angle with the former. The eustachian tubes are visible. There is a well-marked depression just posterior to the ridge which runs across and joins the two alaparasphenoids. Much of the basioccipital is broken, but the occipital condyle, although eroded, is still present and was small. The foramen magnum is directed posteroventrally, but its exact shape is impossible to determine. The profile of the occiput in this view is relatively flat with a slight swelling around the foramen magnum. the foramen magnum.

The occiput is also damaged about the mid-line, but the shape is broadly crescentic, with a well-defined median ridge running down the parietals and supraoccipital to meet the dorsal rim of the foramen magnum in the mid-line. Either side of this ridge there is a well-marked groove, which probably indicates the border between the supraoccipital and opisthotic. There appear to have been no foramina in the supraoccipital. The temporal fossae are distinct from this angle and their posterior border forms a well-defined ridge along the upper edge of the occiput. The fossae do not, however approach the mid-line.

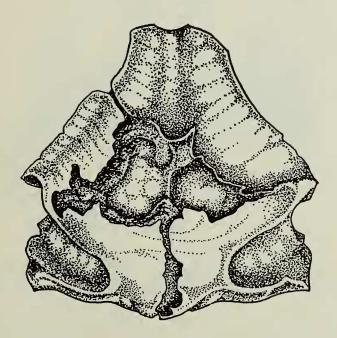
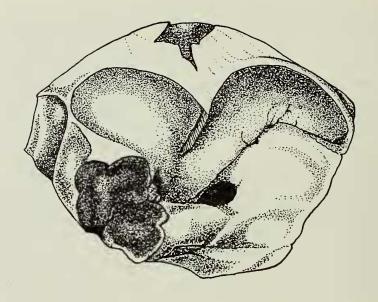


Fig. 1. Halcyornis toliapicus. BM(NH) No. A 130. Cranium. Dorsal View, ×4.



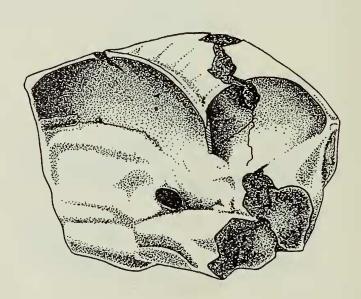


Fig. 2. Halcyornis toliapicus. BM(NH) No. A 130. Cranium. Lateral View, ×4.

MEASUREMENTS

Maximum width across exoccipital region		20.5	mm
Minimum width between temporal fossae		9	mm
Width between postorbitals		22	mm
		7	mm
Minimum width of interorbital septum.		2	mm
Maximum depth of skull in orbital region		17	mm
Maximum length of auditory meatus .		9	mm

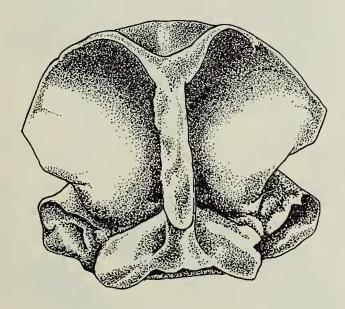


Fig. 3. Halcyornis toliapicus. BM(NH) No. A 130. Cranium. Frontal View, ×4.

III. COMPARISON WITH RECENT FORMS

From the description it is apparent that for determining relationships, characters might be used other than those used in the past. The most obvious of these relate to:

- I. The upper edges of the orbit.
- 2. The interorbital septum and foramen.
- 3. The relative size and shape of the parasphenoid region.

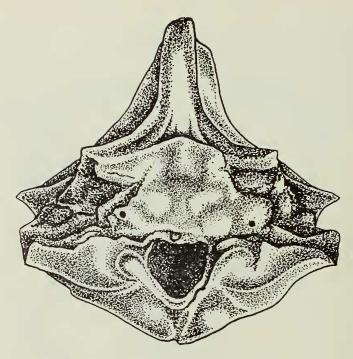


Fig. 4. Halcyornis toliapicus. BM(NH) No. A 130. Cranium. Ventral View, ×4.

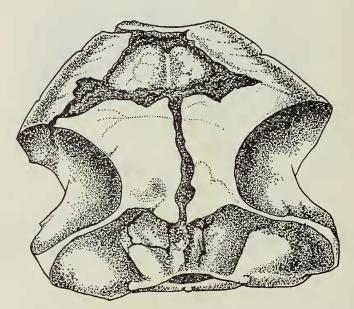


Fig. 5. Halcyornis toliapicus. BM(NH) No. A 130. Cranium. Posterior View, ×4

I. The edges of the orbit

Lydekker's views on the affinities of *Halcyornis* appear to have been strongly influenced by his opinion that the appearance suggested the presence of supraorbital grooves, subsequently destroyed. On birds which normally live on or by salt water,

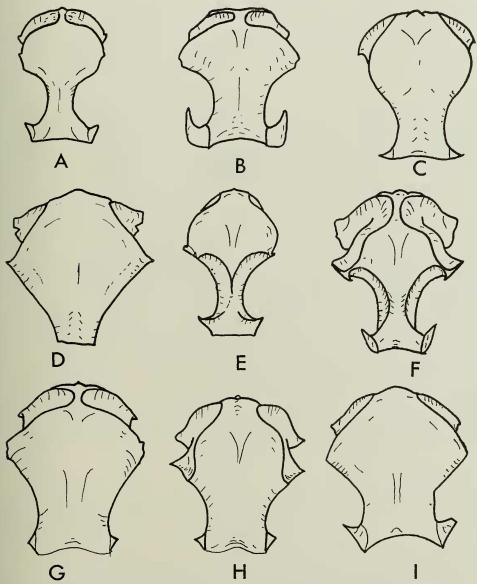


Fig. 6. Diagrams of dorsal views of crania to show width of interorbital bridge. A, Alcedo; B, Dacelo; C, Coccyzus; D, Halcyornis; E, Larus: F, Puffinus; G, Rhynochetos; H, Fregata; I, Coracias.

the supraorbital glands tend to become greatly enlarged and are housed in distinct grooves along the upper edges of the orbits (Text-fig. 6E, F). These glands, which assist salt-excretion, are much smaller in related fresh-water species. The grooves, where present, are on top of the skull and tend to occupy most of the upper edges of the orbits, reducing the thickness of the frontal bones in this region. They may be deepest towards the centre of their width, at times penetrating to the orbits below and forming a series of fenestrae, or they may give to the orbital edges an irregular or eroded appearance. A consistent feature is the distinct ridge of bone along the inner edge of each groove where the frontal bone is restored to its normal thickness.

Since these ridges of bone are not apparent on *Halcyornis* it would be necessary, were it held that supraorbital grooves had been present, to assume that the entire bony shelf supporting the supraorbital glands had worn away completely, back to this ridge. Although the presence of the groove reduces the thickness of the frontal bone by removing part of its upper surface, it does not affect the underlying surface within the orbit which curves downwards away from the orbit edge in the normal manner; and therefore an orbit worn back to the inner edge of a supraorbital groove would show a considerable depth of worn or broken surface at the edge between the top of the skull and the inside of the orbit. The skull of Halcyornis does not; the upper edge of the orbit does not taper to a very narrow edge but shows an abrupt surface about one millimetre deep, suggesting that a small amount of wear may have occurred on a normal orbit lacking a supraorbital groove (Text-fig. 2A, B). Another character of the supraorbital grooves is that it tends to terminate rather abruptly posteriorly, with the inner ridge curving towards the orbit edge; thus if a groove were to wear away, the orbit edge would show a sharp discontinuity at this point. is no such discontinuity in Halcyornis.

The absence of a supraorbital groove suggests that the specimen is not related to the Procellariiformes, Anseriformes or Charadriiformes (including Laridae). The Pelecaniformes (Text-fig. 6H) and Ciconiiformes, although in some cases associated with salt water, do not possess these supraorbital grooves. Since the groove is a relatively plastic and adaptable character in the families in which it now occurs, it might be argued that it could have been absent in some or all species in earlier epochs. It is known to be present in Miocene gulls but we have no definite proof that it was present earlier, and as an indication of relationship it can be assessed only in conjunction with other characters.

2. The interorbital septum

Halcyornis has a thick, unfenestrated interorbital septum (Text-fig. 3) with a single optic foramen in a low posterior position (Text-fig. 7I). Most of the birds discussed in this paper have marked and often extensive interorbital fenestrae (Text-fig. 7); these include the Procellariiformes, Pelecaniformes, Ciconiiformes and Charadriiformes. In the skimmers (Rhynchops spp., Charadriiformes) a highly specialized method of feeding (Zusi, 1962) has necessitated extra strengthening of the skull, including the development of a thick, solid interorbital septum; the latter, however, is pierced by the optic foramen in a high position (Text-fig. 7C) and there are small paired fenestrae opening into the cranial cavity just above this. Inter-

orbital fenestrae are also present in the Rhinochetidae, Cuculidae, and Alcedinidae. On the other hand the coraciiform and piciform families listed earlier generally show a solid interorbital septum with a low posterior optic foramen like that of *Halcyornis*; the only exceptions are the Upupidae with a pair of fenestrae opening into the cranis; to cavity from the upper orbits and the Momotidae with a tiny variable "relict" foramen in the mid-septum. On the basis of this character there is a strong case for linking *Halcyornis* with the Coraciiformes and Piciformes, although the example of *Rhynchops* indicates that exceptional circumstances could lead to some adaptive variation in the fenestration of the septum.

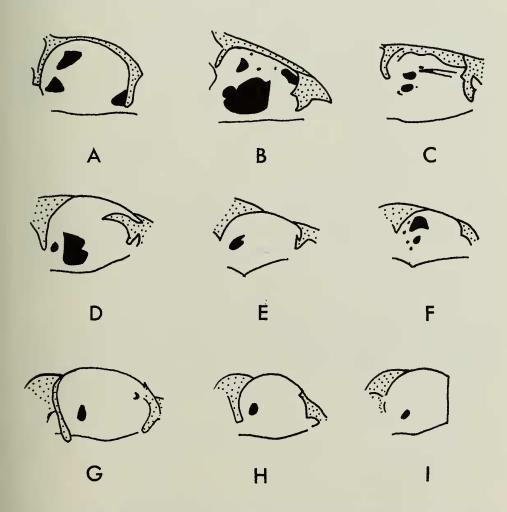


Fig. 7. Diagrams to show interorbital septa and position and size of interorbital foramina. A, Fregata; B, Puffinus; C, Rhynchops; D, Dacelo; E, Merops; F, Upupa; G, Leptosomus; H, Eurystomus; I, Halcyornis.

Another character in which *Halcyornis* resembles species of the Coraciiformes and Piciformes is the shape of the angle formed by the interorbital septum and the underside of the interorbital bridge section of the frontals (Text-fig. 8). On most of the Recent species examined the interorbital bridge is relatively thin and the septum extends well up towards the orbit where it meets the underside of the frontal at a sharp angle. In Halcyornis the interorbital bridge is much thicker towards the mid-line and tapers down more gradually, making an obvious junction with the septum at about a third of the distance between the top of the bridge and the base of the septum (Text-figs 2A, 2B, 3). This is less obvious anteriorly where the bone narrows, but can be clearly seen in lateral view as a discontinuity crossing the inner orbit. This heavier tapering interorbital bridge is apparent on skulls of Momotus (Coraciiformes) and Megalaima, Selenidera and Monasa (Piciformes). Eurystomus, Leptosomus and Merops (all Coraciiformes) show a similar low junction between septum and frontal inside the orbit; in these genera, however, there is a mid-line hollow on the top of the skull and the frontal is concave in cross-section, so that the apparently lower position of the junction is due to a general ventral displacement and cannot be regarded as an homologous development.

3. The parasphenoid region

We have followed Jollie (1957) in regarding the externally visible ventral bones of the hind-skull as parasphenoid rather than sphenoid. The basiparasphenoid of Halcyornis is transversely elongated and roughly oblong, with a slight lateral taper (Text-fig. 4, Pls 1B, 3E). It is rather flat and this may have been emphasized by pressure and slight erosion. Anteriorly it terminates in a distinct edge where it abuts on the alaparasphenoids. The rostroparasphenoid is thick and has a small but distinct ventral prominence near the posterior end. The most conspicuous feature on each side is the alaparasphenoid, directed strongly laterally at the hind end of the rostroparasphenoid to form a prominent bulging ridge at the back of the base of the orbit, curving upwards to meet the orbitosphenoid. The lateral ends of both alaparasphenoids and the basiparasphenoids are broken away.

In the Procellariformes (Pl. 3C) the basiparasphenoid tapers markedly towards the front and there is a narrow gap between it and the ventrally projecting edge of what appears to be the orbitosphenoid. The Pelicaniformes show a tapering basiparasphenoid which becomes distinctly wedge-shaped in some forms, and in Fregata (Pl. 3B) there is again a gap between the basiparasphenoid and orbitosphenoid. In the Charadriiformes (Pl. 3D, F) this anterior taper is again apparent on the basiparasphenoid, while the alaparasphenoid is more prominent than in the previous taxa but slants away weakly to the orbital and otic region, least so in some small Larus species such as L. ridibundus. The Cuculiformes (Pl. 3L) show a wedgeshaped basiparasphenoid, narrow anteriorly in some species but broad in others,

and the alaparasphenoid is poorly defined.

In these characters, as in the previous ones, the greatest similarity to Halcyornis is shown by piciform and coraciiform birds. In most of these the basiparasphenoid is wide transversely, tending towards an oblong shape with little lateral taper; in the Capitonidae (Piciformes) and in the Coraciidae (Pl. 3H) Leptosomatidae, and

Momotidae (Coraciiformes) it has a similar shape to the fossil, but in the Bucconidae (Pl. 3I) and Galbulidae (Piciformes) and in the Alcedinidae (Pl. 3J) and Meropidae (Pl. 3G) (Coraciiformes) the distance between the orbits and the foramen magnum is shortened, making the basiparasphenoid narrower from front to back.

In both orders many species have a pair of small prominences on the ventral surface of the basiparasphenoids. These are very variable, being almost absent, for instance, on Alcedo (Alcedinidae). In Halcyornis this bone shows a pair of small areas with dull surfaces suggesting abrasion or heavy pressure, corresponding in position to these prominences although one is a little displaced by fracture.

The principal difference between the Piciformes and Coraciiformes lies in the development of the Alaparasphenoid. On the piciform skulls examined this element is barely apparent, although there is a small, poorly developed ridge on the skulls of the larger Megalaima species. In the Coraciiformes the alaparasphenoid shows some variation in development in the Meropidae, Leptosomatidae, and many of the Coraciidae it is well developed, as a distinct projecting ridge at the posterior basal edge of the orbit, the resemblance to Halcyornis being especially strong in the rollers Leptosomus, Eurystomus and Coracias.

In both orders the rostroparasphenoid is relatively stout; Merops (Meropidae) and Dacelo (Alcedinidae) show a ventral prominence near the posterior end which is like that on the fossil.

Conclusions

The characters of Halcyornis listed above afford no good reason for linking it with either the Laridae or the Charadriiformes. The only orders with which it appears to show any consistent affinities are the Piciformes and the Coraciiformes; insofar as the parasphenoid region is concerned it seems more like the Coraciiformes, in particular the Coraciidae and the Meropidae.

IV. DETAILED COMPARISON WITH CORACIIFORM AND PICIFORM SPECIES

The species within these two orders do not show uniform skull characters, for they have evolved differences in feeding habits and bill-shape and therefore exhibit varying degrees of divergence from a hypothetical ancestral form. Specimens of the following species were used in this comparison:

CORACHFORMES

Alcedinidae

Dacelo novaeguineae Alcedo atthis

Momotidae

Momotus sp. Aspatha gularis Baryphthengus ruficapillus Meropidae Merops apiaster

Leptosomatidae
Leptosomus discolor
Coraciidae
Atelornis pittoides
Coracias garrulus
Eurystomus glaucurus
Upupidae
Upupa epops

PICIFORMES

Galbulidae
Galbula leucogastra
Bucconidae
Monasa morphoeus
Capitonidae
Megalaima virens
M. haematocephala
Ramphastidae
Selenidera langsdorffi

1. Cranial shape

The general roundness of the fossil cranium in lateral view (Text-fig. 2A, B) is similar to that of Monasa morphoeus, Megalaima haematocephala (Text-fig. 8B), Selenidera langsdorffi and the Momotidae species. Most of the others have a cranium extending further back and with a slight upward taper, apparently caused by a forward shift of the foramen magnum and a shortening of the basiparasphenoid area so that the occiput faces more ventrally. This shift of the foramen would seem to be linked with a more upright perching stance by the bird. In Leptosomus and Eurystomus this shift is accompanied by a shortening of the cranium but this appears to be compensated for by an increase in the height, the cranium bulging noticeably at the top. In Upupa there is no apparent shift but the cranium is generally enlarged and rounded.

2. Temporal fossae

It has already been indicated that the size and shape of the temporal fossae (site of origin of the M. adductor mandibulae externus) varies considerably from species to species. The two examples of *Megalaima* demonstrate this. The fossae of the smaller species (M. haematocephala, Text-fig. 8B) are little larger than those of *Halcyornis*, but those of the larger bird (M. virens, Text-fig. 8D) are considerably elongated and extend across to meet at the back of the skull. In the Coraciiformes small fossae similar in size to those of *Halcyornis* but differing a little in shape occur on the various Momotidae species (Text-fig. 8C). In *Leptosomus* they are also small, but on other species show a variable tendency to become elongated towards the mid-line, almost meeting in *Atelornis pittoides* and the Alcedinidae (Text-figs 6B, 8F). The temporal fossae of *Halcyornis* extend well forwards anterodorsally,

approaching the orbit closely and reducing the spur above the postorbital process to a narrow ridge. A slight discontinuity in the floor of the fossae, adjacent to the process, seems to indicate a secondary area of muscle attachment, probably of the M. dermotemporalis, an accessory muscle of the neck used in head movements. This area is relatively poorly developed in most of the forms considered here but is rather more apparent in Megalaima haematocephala, Monasa morphoeus and Upupa epops, although very shallow in Upupa. The narrower ridge of the postorbital process in Leptosomus discolor and Selenidera langsdorffi appears to be due to an

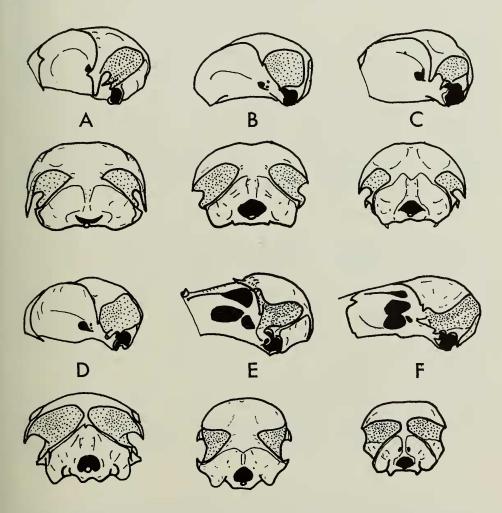


Fig. 8. Diagrams of left lateral posterior views of crania to show variation and extent of temporal fossae. A, Coracias; B, Megalaima haematocephala; C, Momotus; D, Megalaima virens; E, Larus; F, Alcedo.

increase in the M. adductor mandibulae externus rather than M. dermotemporalis. The relatively small size of the M. dermotemporalis in the species which actively hunt live prey, and its development in species which tend to take insects from a solid substrate or to take fruit, suggests that the relatively plastic shape of the fossae is linked with the type of feeding behaviour.

3. Interorbital bridge and dorsal groove

Dorsally the cranium of *Halcyornis* tapers to a relatively narrow interorbital bridge formed by the frontals (Text-fig. 1), and there is a distinct groove along the mid-line (Text-fig. 3, Pl. 1A). The skull roof also bears a series of fine striae radiating from the edges of the orbits, mostly directed posteriorly (Text-fig. 1).

Over the two orders as a whole the trend appears to be for the interorbital bridge to become gradually broader (Text-fig. 6). The bridge is fairly narrow on Aspatha gularis and Atelornis pittoides, but only in Blcedo atthis (Text-fig. 6A) does it approach the narrowness of Halcyornis. Milne-Edwards and Grandidier's (1876) plate of the skull of the Madagascan Roller, Bractypteracias leptosomus (Coraciidae), shows that this too had a narrow interorbital bridge. In the Alcedinidae the width of the bridge varies (Text-fig. 6A, B), the narrow bridge apparently correlated with a slender bill. The dorsal groove is apparent in species of Momotidae, Alcedinidae, Upupidae, Leptosomidae and most Coraciidae; poorly defined in Atelornis pittoides, Monasa morphoeus and Merops apiaster; virtually absent in the Ramphastidae;

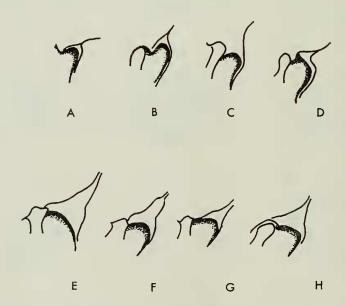


Fig. 9. Diagrams of the left external auditory meatus. A, Halcyornis; B, Eurystomus glaucurus; C, Leptosomus discolor; D, Coracias garrulus; E, Dacelo novaeguineae; F, Megalaima virens; G, Monasa morphoeus; H, Momotus martii; approx. ½ nat. size.

and replaced by a ridge in the Galbulidae and Capitonidae. The striae, which we suspect may vary with age and the degree of ossification, are more or less apparent in most of these species.

4. Occipital region

The fossil shows a very definite curved occiput of fairly even width (Pl. IC). The lateral ends (formed by the exoccipitals) terminate in a narrow ridge which is also the posterior edge of the auditory meatus, and this ridge curves abruptly at the top to form a small arch almost at the point where the ridge of the upper edge of the occiput terminates.

Most of the skulls examined show an occiput similar to that of *Halcyornis*, but its degree of curvature varies from one species to another. On most of them the ridge of the upper edge of the occiput terminates laterally in a triangular-shaped surface which slopes down towards the meatus, the upper arch of which is less acute than in *Halcyornis*, lower and more anterior in relation to the exoccipitals. The rollers *Eurystomus glaucurus* and *Coracias garrulus* (Text-fig. 8A), however, are much more like *Halcyornis*. Firstly, the occiput is very similar in shape and relative size; secondly, in *E. glaucurus* and to some extent in *C. garrulus* the triangular surface is very small and the upper edge of the meatus terminates in a small acute arch, near the end of the occipital ridge, very similar to that of *Halcyornis* (Text-fig. 9). In the latter some allowance must be made for probable erosion of these surfaces.

V. POSSIBLE CHARACTERS OF HALCYORNIS

When a fossil bird is known only from an incomplete skull, any ideas concerning its appearance or habits must necessarily be highly conjectural. It is, however, possible to make a few intelligent guesses by extrapolation from Recent species. The size of the fossil skull, compared with those of other birds, suggests that *Halcyornis* was probably about the size of a medium-sized thrush (*Turdus* sp.). The position of the foramen magnum suggests that the bird did not have the very upright posture of the present-day rollers (Coraciidae) and kingfishers (Alecinindae) but probably adopted a more horizontal body posture on a perch or on the ground, like that of the smaller barbets (Capitonidae). The narrow bridge between the orbits suggests that the bill was probably slender and more like a typical kingfisher's than a roller's. Most birds of this type which catch living food by rapid and vigorous movements have temporal fossae extending well back around the skull; but the temporal fossae of *Halcyornis* are fairly small and rounded, suggesting that this species may have taken food, probably small creatures or fruit, from the substrate or from the surfaces of vegetation rather than by seizing it rapidly in the air.

VI. GENERAL CONCLUSIONS

From an examination of affinities within the higher taxa it is apparent that *Halcyornis toliapicus* has been wrongly assigned to the Laridae and that its true affinities seem to lie with the Coraciiformes and Piciformes, more specifically with the former. The subsequent comparison with families within those two orders

appears to confirm that conclusion and to reinforce the view that the closest affinities are with the Coraciidae. The similarities are not sufficient, however, to justify referring it to that family, and it appears to show the characters of several families, and also exhibits its own peculiarities and combination of characters. Hitherto Coraciiformes have not been described from the Lower Eocene, but the momotid *Uintornis*¹ has been described from the middle Eocene of Wyoming, the bucerotid *Geisleroceros* from the Middle Eocene of Germany, the coraciid *Geranopterus* from the Upper Eocene of France, and the alcedinid *Protornis* from the Upper Eocene of Switzerland. *Halcyornis*, because of its earlier origin, might be a representative of a group ancestral to more than one of the Recent families. As a matter of taxonomic convenience it seems best for the present to treat *Halcyornis* as the unique representative of a new family of the Coraciiformes, systematically not far removed from the Coraciidae: the Halcyornithidae.

VII. SYSTEMATIC DESCRIPTION Order CORACHFORMES

Family HALCYORNITHIDAE nov.

Family diagnosis: Cranium not particularly inflated or rounded. Interorbital bar narrow and deep. Postorbital process small and narrow. Temporal fossae tapering posteriorly, occupying about two-thirds of total width of cranium, slightly curved where they border the edge of exoccipital region. Occiput semi-lunar with well-defined median ridge on parietals. Interorbital septum thick, with single optic foramen in low position. Wide angle between alaparasphenoids and rostroparasphenoid, latter thick.

Genus HALCYORNIS Owen, 1846

DIAGNOSIS: The only genus of its family.

Type species: Halcyornis toliapicus (Koenig).

Halcyornis toliapicus (Koenig, 1825) (Pls 1-3; Text-figs 1-9)

1825 Larus toliapicus Koenig, pl. 16, fig. 193.1846 Halcyornis toliapicus (Koenig): Owen: 554.

Diagnosis: The only species of the genus.

HOLOTYPE: Imperfect cranium in Brit. Mus. (Nat. Hist.) No. A 130.

LOCALITY AND HORIZON: London Clay (Ypresian), Lower Eocene of Sheppey, Kent, England.

¹According to Dr. J. Cracraft (pers. comm.), Uintornis is not a motmot.

VIII. ACKNOWLEDGEMENTS

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IX. REFERENCES

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C. J. O. Harrison, Ph.D.
Department of Zoology,
Sub-department of Ornithology,
Zoological Museum,
Tring,
Herts.

C. A. WALKER,

Department of Palaeontology

BRITISH MUSEUM (NATURAL HISTORY)

CROMWELL ROAD,

LONDON, SW7 5BD